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Material type and roughness influence structure of intertidal communities on coastal defences

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Abstract

On a global scale, urbanisation has resulted in substantial proportions of the coast being replaced by artificial structures such as marinas, breakwaters or seawalls. There is broad consensus that coastal defence structures are poor surrogates of the natural habitats they replace. Here we investigate the effect of the type and roughness of materials used for the construction of artificial structures on the biota by comparing abundances and distribution of key intertidal taxa between natural shores and coastal defences. Lower abundance of gastropods and barnacles were found on artificial coastal defence structures (regardless of the material type). At small–spatial scales, there was a significant effect of roughness which increased the abundances of key taxa. Results suggest that choice of materials used for the construction of coastal defence structures *per se* has little effect on community structure, but that enhanced roughness could make coastal defences better surrogates of natural habitats by supporting assemblages that are more similar to those found on natural shores.

Keywords: artificial structures, intertidal assemblages, marine biodiversity, urbanisation, macroalgae

37 **Introduction**

38 The extent of natural coastal habitats converted for urban use, including the construction of
39 coastal defence structures such as seawalls, breakwaters or groynes, is increasing globally
40 (Goodsell 2009; Firth *et al.* 2013). This trend is likely to continue, given predictions for sea
41 level rise and increased storminess (Thompson *et al.* 2002; Wong *et al.* 2014). There is thus
42 a clear interest in understanding the environmental consequences of these artificial habitats
43 (Moschella *et al.* 2005), with several studies highlighting the importance of understanding
44 the underlying ecological processes (Moreira *et al.* 2006; Munari 2013) when planning
45 developments along shores (Chapman & Bulleri 2003).

46 Construction of artificial structures provides additional hard substrata for epibenthic
47 organisms. These structures, however, can have a strong effect on the structure and
48 functioning of flora and fauna assemblages in adjacent hard- or soft-bottom habitats (e.g.
49 Martin *et al.* 2005; Martins *et al.* 2009; Bertasi *et al.* 2007). Moreover, although epibiotic
50 communities on artificial structures can be qualitatively similar to those on natural rocky
51 shores, differences in the diversity, abundance, behaviour and/or phenology of epibiota on
52 breakwaters, seawalls or groynes have been reported by many authors (e.g. Chapman 2003;
53 Chapman & Bulleri 2003; Bulleri *et al.* 2004; Moschella *et al.* 2005; Moreira 2006;
54 Moreira *et al.* 2006; Martins *et al.* 2009; Firth *et al.* 2013). Collectively, these studies
55 suggest that artificial structures cannot generally be considered surrogates of the natural
56 habitats they replace.

57 Some studies consider that artificial structures built with locally quarried materials are
58 likely to have minimal effect on intertidal assemblages, and therefore predict that the

epibiotic communities on those structures would be similar to those colonizing nearby natural rocky habitats (see Thompson *et al.* 2002; Branch *et al.* 2008). However, there is evidence that this is not always true and differences have been found between assemblages on natural habitats and artificial structures made of locally quarried rock (see Bulleri & Chapman 2010, for review). Moreover, current literature on the effects of coastal urbanisation includes ambiguous results, revealing both positive and negative effects on the maintenance of local populations. For instance, the outcomes of investigations on the effects of coastal urbanisation on the distribution of limpets have been variable. Some authors (Moreira *et al.* 2006; Díaz–Agras *et al.* 2010) found no differences in the abundance or frequency of occurrence of limpets inhabiting artificial substrata and rocky shores, while other authors reported greater numbers of limpets on either natural (e.g. Bulleri & Chapman 2004; Bulleri *et al.* 2004) or artificial structures (Guerra–García *et al.* 2004).

Modification of artificial structures to make them better surrogates of natural habitats is a form of mitigation that is receiving increasing attention (Moreira *et al.* 2007; Chapman and Blockey 2009; Martins *et al.* 2010; Firth *et al.* 2013). Some attempts to reduce their ecological impacts have been addressed by adding elements (e.g. wetland vegetation) or features of habitat (e.g. rock-pools) that are absent from urban structures (Zedler & Leach 1998; Bulleri & Chapman 2010). Natural rocky shores differ from artificial structures in a number of important features (Chapman and Blockey 2009; Firth *et al.* 2013) namely differences in material composition and structural roughness, and there is now a substantial body of work highlighting the important role of substratum heterogeneity in structuring intertidal communities (Thompson *et al.* 1996; Pinn *et al.* 2008; Griffin *et al.* 2009; Skov *et*

82 *al.* 2011; Gartner *et al.* 2013). Artificial structures generally fail to provide the array and
83 diversity of habitat heterogeneity found on most natural shores (Chapman 2006; Firth *et al.*
84 2013; Browne & Chapman 2014). For instance, seawalls generally lack microhabitats such
85 as rock pools that retain water during low tide allowing the establishment specialist species
86 (Chapman & Blockley 2009; Firth *et al.* 2013; Browne & Chapman 2014). Likewise,
87 seawalls or groynes have steep inclinations, which reduce the areal extent of the intertidal
88 zone compared to the generally gentler slope of natural habitats (Moreira *et al.* 2007;
89 Bulleri & Chapman 2010). Therefore, we hypothesize that artificial structures with rougher
90 surfaces, i.e., more similar to natural habitats, will benefit intertidal species, at least those
91 small-sized which can easily find refuge from the harsh intertidal conditions.

92 The ecological impacts of coastal infrastructure in shallow coastal waters may vary
93 accordingly with the nature of the surrounding habitat (Bulleri & Chapman 2010). Most of
94 the research to date has considered coastal defences that lie behind soft sedimentary
95 shorelines that are at risk from erosion (Gacia *et al.* 2007), thus providing additional hard
96 surface for colonization by benthic organisms where it was previously absent (Chapman &
97 Bulleri 2003; Moschella *et al.* 2005). This study was conducted in the Azores, an oceanic
98 archipelago where volcanic rubble and steep cliffs constitute the most common marine
99 habitats. In the Azores, most artificial structures are used to protect nearby towns from high
100 sea levels during winter storms. In contrast to many other locations worldwide, coastal
101 defences in the Azores are typically built on top of former natural stretches of rocky coasts,
102 thus showing similarities in physical nature (i.e., hard substrate) to adjacent natural
103 environments. Therefore, unlike areas where artificial structures are deployed on soft-
104 bottom areas, we hypothesize that assemblages on most of the Azorean artificial structures

will be of similar composition to those found on adjacent natural environments. However, given the well known effect of substratum type in structuring intertidal assemblages (e.g. Connell & Glasby 1999; Glasby 1999), the first objective in this study was exactly to compare patterns of distribution and abundance of intertidal organisms on natural rocky shores with that of coastal defence structures (boulders and blocks) made of either basalt (locally quarried rock) or concrete (a non–natural substratum, and probably the most common material used in coastal urbanisation). We are interested in testing if using rocks that were locally quarried would somehow minimise the impacts of coastal urbanisation. In addition to this, we also investigated how natural small-scale variability in substratum topography (within artificial structures made of basalt) influences the structure of intertidal assemblages. We predict that areas of the substratum with rougher topography will support assemblages that differ from those found in areas of the substratum with smoother topography.

This information will help to understand the effects of hard defence structures, and may be potentially provide information that can be used to mitigate the ecological impacts of coastal urbanisation (e.g. Martin *et al.* 2005; Moschella *et al.* 2005; Martins *et al.* 2010).

Material and Methods

The study was conducted on São Miguel Island (Azores, Fig. 1), where maximum tidal range is approximately 2 m and the coast is exposed to medium to high levels of wave action. In general, three zones can be recognized in the São Miguel Island rocky intertidal, following classical zonation schemes (Stephenson & Stephenson 1972): the low–shore is characterized by a covering of coarsely branched, coralline and turf–forming species of

macroalgae; the mid–shore is dominated by the barnacle *Chthamalus stellatus*, whereas the gastropod littorinids *Tectarius striatus* and *Melarhaphe neritoides* usually inhabit in the upper–shore (Martins *et al.* 2008b).

To characterize the intertidal assemblage community composition and abundance, sampling was carried out on natural rocky shores of basaltic nature (hereafter referred to as Natural shore), and artificial coastal defence structures built of either basalt (hereafter Basalt artificial structures) or concrete (hereafter Concrete artificial structures) located along the coastline of São Miguel (176 km perimeter, length 65 km, width 8–15 km) (Fig. 1). Only the seaward sides of natural and artificial habitats were sampled to standardize for wave exposure. Five locations representative of the three habitat types (Natural shore, Basalt artificial structures and Concrete artificial structures) were randomly selected (Fig. 1). All locations were separated by tens of kilometers and similarly exposed to incoming oceanic swell. Within each location, five replicate quadrats (25x25 cm) were randomly placed at least 2 m apart on emergent substrata at low–, mid– and upper–shore levels, visually determined by the presence of macroalgae, barnacles and littorinid respectively. The assemblage structure was hence assessed at each level. Percentage cover of sessile organisms (e.g. macroalgae, barnacles) and bare rock (a measure of unoccupied space) were obtained following the methodology described in Dethier *et al.* (1993), in which the abundance of organisms within each of the 25 5x5 cm sub–quadrats (that add up a sampling quadrat) was assigned a score ranging between 0 (absent) and 4 (100% cover of the sub–quadrat). Total percentage cover is then estimated by summing the scores of all sub–quadrats (see Dethier *et al.* 1993 for further details). Macroalgae were identified and grouped into distinct morpho–functional groups (FGs), based on species’s morphology and

the way they compete for resources (Steneck & Dethier 1994; Arenas *et al.* 2006; Veiga *et al.* 2013). The selected FGs were: Ephemerals (considering first colonizers, including diatomaceous biofilms, microalgae and filamentous algae such as *Chaetomorpha*, *Cladophora*), Foliose (e.g. *Porphyra*, *Ulva rigida*), Coarsely branched (e.g. *Caulacanthus ustulatus*), Coenocytic (*Codium adhaerens*), Articulated calcareous (e.g. *Corallina elongata*), Leathery (e.g. *Fucus spiralis*), Calcified crustose (e.g. *Lithophyllum*), and Non-calcified crustose (e.g. *Nemoderma*). Taxa present within quadrats but not reaching a score of 1 were given a nominal value of 0.5%. Motile invertebrates were identified up to species level, counted and expressed as number of individuals per quadrat. All surveys were made between the 24th June and 4th August 2013, during low–water spring tides.

A complementary small-scale study investigated the role of substratum roughness in determining patterns of species distribution on coastal defence structures by comparing the abundance of organisms in blocks with smooth and rough surfaces visually selected *a priori* on a basalt seawall at two sites selected 10's of meters apart. Five replicate plots on smooth *vs.* rough blocks were sampled. In this case, only mid– and upper–shore was sampled in this survey, since low–shore roughness was hidden by dense macroalgal dominance. A pin–microrelief method (Vázquez *et al.* 2009) was adapted to measure substratum random roughness (RR) in the sampled plots. Differences in substratum surface height were recorded in 15 cm transects with spacing between readings of 2.5 mm, and RR index was calculated as the standard error among heights (Allmaras *et al.* 1966). This survey was made between August 12th and September 12th 2014, during low–water spring tides. Sampling of the biota was done as described above.

Data analysis

173 Multivariate analysis.

174 Differences in the structure of assemblages were investigated for each tidal height using a
175 two-way permutational analysis of variance (PERMANOVA) with habitat (Ha, fixed, with
176 three levels: Natural shores, Basalt artificial structures and Concrete artificial structures)
177 and location (Lo, random, nested in habitat, with five levels) as factors. PERMANOVA
178 analyses were run on Bray Curtis similarity matrix of both untransformed and presence–
179 absence transformed complete epibenthic assemblage (i.e. including percentage cover of
180 macroalgae/barnacles and abundance of gastropods). Pair-wise tests were used to compare
181 the effects within significant factors.

182 Univariate analysis.

183 The numbers of macroalgal FGs as well as the relative abundance of taxa were compared
184 among habitats following the same procedure as described before but using, in this case,
185 traditional analysis of variance. Prior to analyses, Cochran’s test was used to detect
186 heterogeneity of variances and data were transformed where appropriate (Underwood
187 1997). When homogeneity of data was not achieved after transformation, analyses were run
188 on the untransformed data but using a more conservative significance level ($P < 0.01$)
189 (Underwood 1997).

190 The role of roughness in determining small-scale patterns of species distribution in hard–
191 defence structures, namely the abundance of gastropods and the percentage cover of
192 barnacles, was also investigated using an approach similar to that described above, but
193 including roughness (Ro, fixed, two levels: Smooth and Rough) and site (Si, random, two
194 levels) as factors.

Multivariate analyses were run using PRIMER 6 statistical package with the PERMANOVA+ add-on (PRIMER-E, Plymouth Marine Laboratory, UK), whereas univariate analysis were run using GMAV5 (University of Sydney).

Results

Multivariate analysis.

Assemblage structure (both on the untransformed, Table 1a, and presence-absence data, Table 1b) did not differ significantly among habitats (i.e., Natural shore, Concrete and Basalt artificial structures) on the lower-shore. On the mid-shore, assemblage structure differed significantly between Natural and Basalt when considering abundance data (Table 1a), but not when considering only compositional data (Table 1b). Significant differences on the assemblage structure were detected between Natural shores and both artificial habitats (Concrete and Basalt artificial structures) on the upper-shore, when considering abundance (Table 1a) but not presence-absence (Table 1b) data.

Univariate analysis.

The numbers of macroalgal FGs were generally similar among habitats at all tidal levels, although differences were found among locations ($P < 0.001$, Table 2, Fig. 2).

At low-shore level, the abundance of macroalgal FG showed no differences among habitats, although differences were found among locations ($P < 0.001$, Table 3, Fig. 3).

At mid-shore level, only coarsely branched algae were significantly more abundant on Natural shores than on artificial reefs (means of 6.0% on Natural vs. 0.8% on Basalt and 0.7% on Concrete artificial structures; Table 3, Fig. 3). The abundance of the remaining

functional groups (coenocytic, foliose, articulated calcareous, leathery and calcified and non-calcified crusts) did not vary significantly among natural shores and basalt and concrete artificial habitats, although differences were always found among locations (Table 3, Fig. 3). The number of both *M. neritoides* and *T. striatus* was significantly greater on natural shores than in artificial structures (Table 4, Fig. 4). Mean numbers of littorinids from 0.08 to 1.6 ind. 0.06 m⁻² were observed on coastal defences, while densities between 10.9 and 12.8 ind. 0.06 m⁻² were observed on natural shores (Fig. 4). The abundance of *Patella* spp. did not significantly differ between habitats (Fig. 4, Table 4), while the cover of *C. stellatus*, was significantly greater on Natural shores compared to Basalt artificial structures (28.3 vs. 5.5 % respectively, Fig. 4, Table 4).

Regarding the upper-shore, significant differences were detected among habitats when considering the percent cover of ephemerals, more abundant on Basalt artificial structures (0.14%) than in Concrete artificial structures (0.04%, Table 3, Fig. 3). Articulated calcareous and calcified crusts showed differences among locations ($P < 0.001$, Table 3, Fig. 3), but not among habitats. The abundance of *T. striatus* significantly differed between habitats (Fig. 4, Table 4), with numbers of 11.8 ind. 0.06 m⁻² in natural shores and 1.5 in artificial structures. The numbers of the remaining faunal species were similar among habitats, although differences were found among locations ($P < 0.05$, Table 4, Fig. 4).

Small-scale effect of substratum roughness.

There were significant differences in substratum roughness between the *a priori* selected smooth vs. rough surfaces, with values of 0.18 ± 0.02 mm (mean \pm SE, $n = 20$) and $0.05 \pm$

0.01 respectively (ANOVA, Mid-shore: $F(1,17)$ (pooled) = 16.13, $P < 0.001$; Upper-shore: $F(1,17)$ (pooled) = 16.22, $P < 0.001$).

At mid-shore level, significant differences were found in the mean abundance of *M. neritoides* and *C. stellatus* between rough and smooth blocks although these effects were site-dependent. *M. neritoides* was significantly more abundant on rough blocks (mean values of 10.4 in rough vs. 0.10 ind. 0.06 m^{-2} in smooth surfaces) at site 1, while *C. stellatus* was significantly more abundant on smooth blocks on both sites (mean cover of 39.4% in smooth vs. 6.8% in rough blocks; Fig. 5, Table 5). The littorinid *T. striatus* was significantly more abundant on rough surfaces at both the mid- and the upper-shore (mean number of 12.3 in rough vs. 0.2 ind. 0.06 m^{-2} in smooth surfaces on mid- and 16.7 vs. 1.0 ind. 0.06 m^{-2} on upper-shore levels; Fig 5, Table 5).

Discussion

As we hypothesized, qualitatively similar assemblages of animals and plants were found on both the coastal defence structures and natural habitats. There were, however, relevant effects of urbanisation on the abundance of some intertidal organisms. For instance, the two littorinid species and the cirripid barnacle were substantially (and significantly) less abundant on the artificial structures. Moreover, this effect was generally similar on defence structures made of either concrete or basalt suggesting that they were not directly influenced by the material type of the substratum *per se*. Results from the small-scale study showed that these species were highly influenced by small-scale variation in roughness. The lower abundance of littorinids found on artificial structures may thus be related to the general lack of microtopographic features that are important as habitat for these molluscs.

This is in accordance with the wider literature showing that littorinids generally tend to aggregate around small-scale features of the substratum (Chapman 1995; Jones & Boulding 1999; Silva *et al.* 2014). Both the physical characteristics of the habitats (roughness; e.g. Gray and Hodgson 2004) and also the presence of *C. stellatus*, could provide refuges for this fauna. As observed by other authors (Silva *et al.* 2014), small gastropods were observed inhabiting the tests of dead barnacles, acting therefore as biogenic microhabitats (Aguilera *et al.* 2014), altering the complexity of the substratum and providing shelter and protection from physiological stress to intertidal organisms (Underwood *et al.* 1983; Jernakoff 1985). Roughness has been also considered an important variable on barnacle settlement (e.g. Chabot & Bourget 1988; Skinner & Coutinho 2005). Barnacles had lower abundance on artificial structures (as observed e.g. by Aguilera *et al.* 2014), but in our case, within the artificial structures the effect of roughness contrasted that found for littorinids (i.e., lower abundance on smooth surfaces). Although we did not expect biotic or abiotic factors to differ between sites within the artificial shore, e.g. chemical cues generated by barnacle adults could be influencing our results, since barnacles are known to respond positively to the presence of conspecifics (Skinner & Coutinho 2005), and we could not separate such effects from those related to roughness.

Due to their key role in intertidal assemblages, changes in limpet abundance among habitats may indirectly influence the distribution of other organisms (Hawkins *et al.* 1992). In the present study, and in contrast with Bulleri & Chapman (2004) or Bulleri *et al.* (2004), although natural habitats supported greater densities of limpets than basalt at low-shore levels, no differences were found on the mid-shore, where limpets are usually more abundant (Martins *et al.* 2010). In this and other systems (e.g. Oliva & Castilla 1986,

Branch & Moreno 1994, Moreno 2001) , substantial harvesting of limpets, a traditionally important source of income for many families (Ferraz *et al.* 2001; Martins *et al.* 2008a) may have masked natural patterns of distribution.

Generally, no differences were found in the number of macroalgal functional groups among habitats. However, a lower number of functional groups tended to be found on the upper-shore on natural shores. These macroalgae vary in consistent ways along physical gradients, including, e.g., wave exposure and desiccation (Menge 2000). Wave splash operates vertically, allowing organisms to extend upwards (Ballesteros & Romero 1988; Hobday 1995). In the case of artificial structures, the steep slope may break waves violently against the artificial structures (Allsop *et al.* 2005), encompassing long-term exposure to waves (wetting gradient, Chappuis *et al.* 2014). This could directly affect the vertical distribution of some functional groups, such as calcified and non-calcified crustose algae. Only on the mid- and upper-shore was the epibenthic assemblage composition of coastal defences different from natural habitats. Unlike results from Bulleri & Chapman (2004) who found compositional differences (differences in species identities) in assemblages on seawalls and adjacent rocky shores, we did not find such compositional differences. In our study system, differences found between natural shores and artificial structures were largely restricted to changes in species abundances (not identity).

Conclusion

Information about patterns of distribution of species in natural and artificial habitats is essential in order to understand the ecological impacts of coastal infrastructures (Bulleri & Chapman 2010). Some studies have suggest that artificial structures provide habitat for

epibiotic communities that are qualitatively similar to those found inhabiting nearby natural reefs (e.g. Branch *et al.* 2008) but quantitative studies (e.g. Moschella *et al.* 2005; Firth *et al.* 2014), have shown artificial structures have significantly lower abundance of gastropods, barnacles and coarsely branched algae, indicating some lack of similarity with natural rocky shores. Our study indicates that roughness, rather than substratum type *per se*, can play a key role in determining the distribution of barnacles and littorinids. Our results indicate that selection of materials with rougher surfaces (i.e. enhanced roughness) when building hard-defence structures may be an effective way to make them more similar to natural substrata, enabling them to support taxa abundance more similar to those found on natural shores.

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Figures

Fig. 1 Sampling locations on Natural shores and Basalt and Concrete artificial structures around São Miguel (Azores).

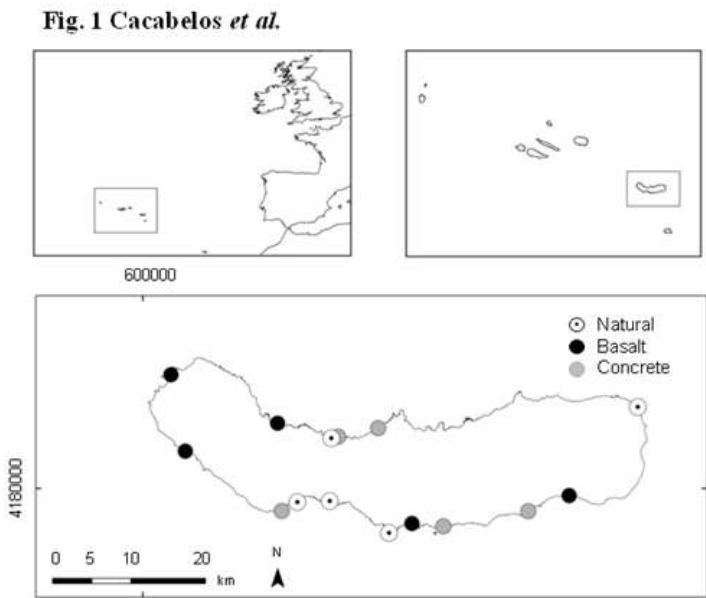


Fig. 2 Macroalgal morpho-functional groups (mean number + SE, $n = 25$) on Natural shores and Basalt and Concrete artificial structures at different intertidal levels.

Fig. 2. Cacabelos *et al.*

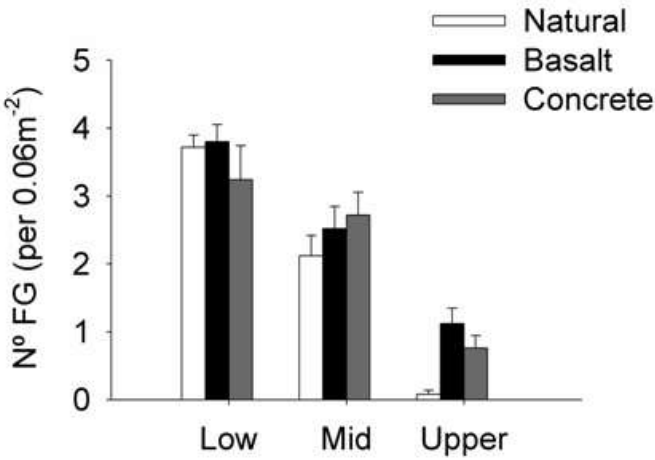


Fig. 3 Covers of macroalgal morpho-functional groups (mean + SE, $n = 25$) associated with Natural shores and Basalt and Concrete artificial structures at different intertidal levels (E, Ephemeral Algae; CB, Coarsely branched; Co, Coenocytic; F, Foliose; AC, Articulated calcareous; L, Leathery; CC, Calcified crustose, NCC, Non-calcified crustose).

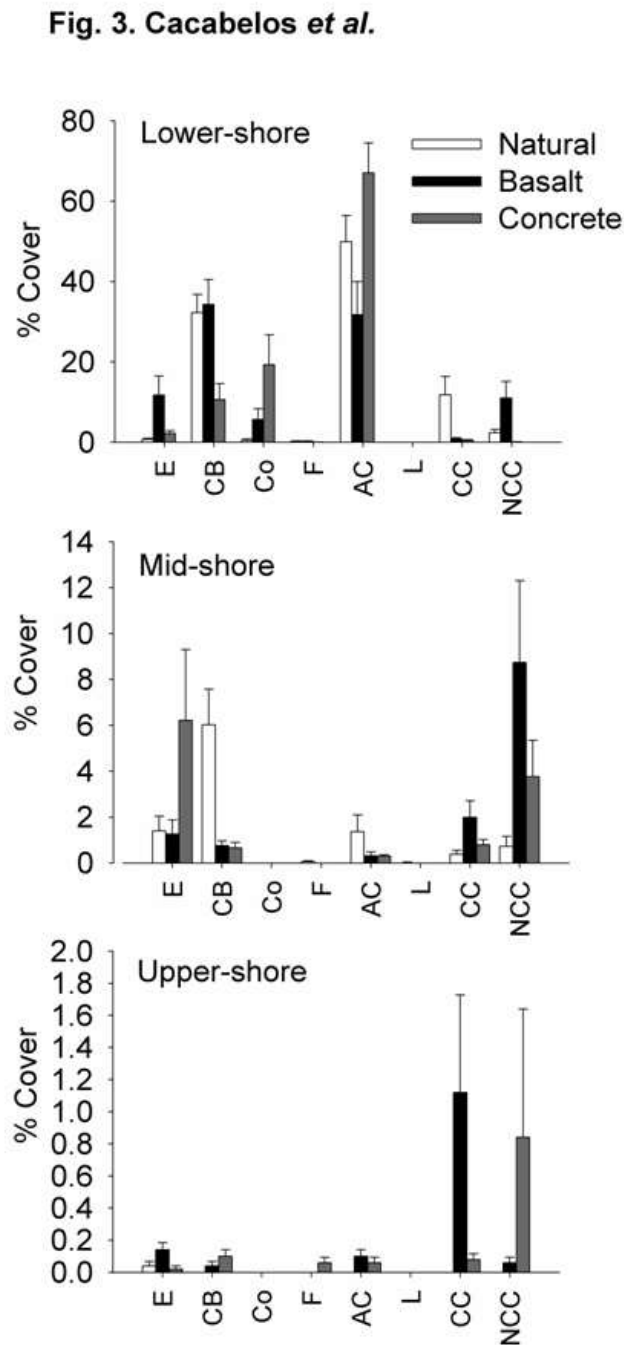


Fig. 4 Gastropod (mean number + SE, $n = 25$) and barnacle (percent cover + SE) abundance associated with Natural shores and Basalt and Concrete artificial structures at mid- and upper-shore (molluscs: T.str, *T. striatus*; M.ner., *M. neritoides*; Pat, *Patella* spp.; barnacle *C. stellatus*, *C.ste.*).

Fig. 4. Cacabelos et al.

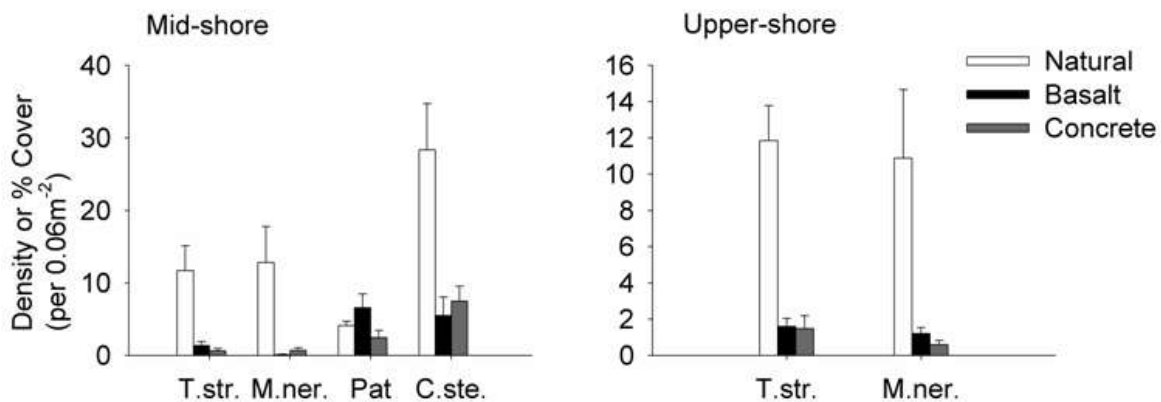


Fig. 5 Gastropod (mean number + SE, $n = 10$) and barnacle (percent cover + SE) abundance associated with rough and smooth surfaces at mid- and upper-shore (molluscs: T.str, *T. striatus*; M.ner., *M. neritoides*; Pat, *Patella* spp.; barnacle *C. stellatus*, C.ste.).

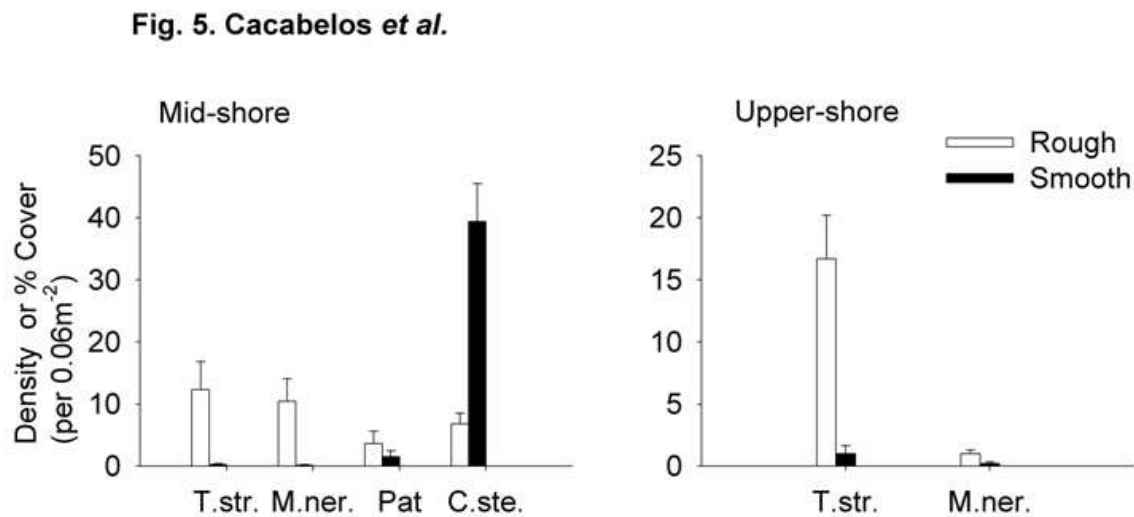


Table 1 Two-way PERMANOVA comparing a) untransformed and b) presence/absence transformed assemblage structure data (including numbers of gastropods and percentage cover of macroalgal functional groups and *C. stellatus*) among habitats (N Natural shore, B Basalt artificial structure, C Concrete artificial structure) and locations (five per habitat, see in Fig. 1) at different intertidal levels.*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

		Low-shore			Mid-shore		Upper-shore	
	Source	df	MS	<i>Pseudo-F</i>	MS	<i>Pseudo-F</i>	MS	<i>Pseudo-F</i>
a)	Habitat	2	13146.0	1.59	13478.0	1.74*	21666.0	4.15**
	Location(Habitat)	12	8291.0	12.47***	7730.1	4.03***	5218.8	4.62***
	Residual	60	665.2		1917.8		1130.4	
	Total	74						
	Pair-wise comparisons					N diff. B*		N diff. B** N diff. C**
b)	Habitat	2	9033.2	1.70	9687.7	1.77	8696.0	1.92
	Location(Habitat)	12	5321.2	6.74***	5480.6	5.25***	4525.9	4.95***
	Residual	60	789.9		1044.4		913.9	
	Total	74						

Table 2 Two-way ANOVA comparing the numbers of macroalgal morpho-functional groups among habitats (Natural shore, Basalt artificial structure, Concrete artificial structure) and locations at different intertidal levels.*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

Source	df	Low-shore		Mid-shore		Upper-shore	
		MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
Habitat	2	2.29	0.49	0.03	0.07	0.90	3.25
Location(Habitat)	12	4.63	4.96***	0.37	4.24***	0.28	5.16***
Residual	60	0.93				0.05	
Total	74						
Cochran's test		ns, 0.1786		ns, 0.2303		ns, 0.232	
Transformation		None		X ^{0.1}		Sqrt(X+1)	

Table 3 Two-way ANOVA comparing the cover of macroalgal morpho-functional groups among Habitats (Natural shores N, Basalt artificial structure B and Concrete artificial structure C) at different intertidal levels. E, Ephemerals; CB, Coarsely branched; Co, Coenocytic; F, Foliose; AC, Articulated calcareous; L, Leathery; CC, Calcified crustose, NCC, Non-calcified crustose.*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. Natural (N).

		df	Low-shore		Mid-shore		Upper-shore	
			MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
	Habitat	2	0.56	0.50	0.39	0.45	0.10	4.77*
	Location(Habitat)	12	1.12	7.03***	0.85	4.04***	0.02	0.76
	Residual	60	0.16		0.19		0.03	
	Total	74						
	Cochran's test		ns, 0.1856		ns, 0.1425		ns, 0.1765	
E	Transformation		X ^{0.1}		X ^{0.1}		None	
	Pair-wise comparisons							B diff. C*
	Habitat	2	4320.10	2.93	8.11	7.82**	0.06	2.11
	Location(Habitat)	12	1473.90	3.27***	1.03	2.40*	0.03	1.64
	Residual	60	450.28				0.02	
	Total	74						
	Cochran's test		ns, 0.2037		ns, 0.2391		$P < 0.05$, 0.2727	
CB	Transformation		None		Ln(X+1)		None	
	Pair-wise comparisons				N diff. B*			N diff. C*
	Habitat	2	2380.3	0.84				
	Location(Habitat)	12	2846.7	44.67***				
	Residual	60	63.7					
	Total	74						
	Cochran's test		$P < 0.01$, 0.5898					
Co	Transformation		None					
	Habitat	2	0.24	0.40	0.03	1		
	Location(Habitat)	12	0.61	4.45***	0.03	6**		
	Residual	60	0.14		0.01			
	Total	74						
	Cochran's test		$P < 0.01$, 0.6341		$P < 0.01$, 1.000			
F	Transformation		None		None			
	Habitat	2	7816.6	1.16	0.44	0.67	0.06	0.79
AC	Location(Habitat)	12	6719.6	21.72***	0.66	4.61***	0.08	9.86***

	Residual	60	309.3		0.14		0.12
	Total	74					
	Cochran's test		ns, 0.2397		ns, 0.1543		$P < 0.01$, 0.4286
	Transformation		None		$X^{0.1}$		None
	Habitat	2	13.52	1.02	17.67	2.15	9.76
	Location(Habitat)	12	13.23	98.5***	8.21	1.97*	6.50
	Residual	60	0.13		4.18		2.40
	Total	74					
	Cochran's test		ns, 0.2174		ns, 0.4581		$P < 0.01$, 0.9806
CC	Transformation		Sqrt(X+1)		None		None
	Habitat	2	1.84	1.98	2.09	2.14	5.49
	Location(Habitat)	12	0.93	6.17***	0.98	6.43***	5.89
	Residual	60	0.15		0.15		5.22
	Total	74					
	Cochran's test		ns, 0.1427		ns, 0.1923		$P < 0.01$, 0.9981
NCC	Transformation		$X^{0.1}$		$X^{0.1}$		None

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Table 4 Two-way ANOVA comparing the numbers of faunal species (density of *T. striatus*, *M. neritoides* and *Patella* spp. and percent cover of *C. stellatus*) among habitats (Natural shores N, Basalt artificial structure B and Concrete artificial structure C) and locations at different intertidal levels.*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

		df	Mid-shore		Upper-shore	
			MS	<i>F</i>	MS	<i>F</i>
<i>T. striatus</i>	Habitat	2	15.96	6.89**	25.43	18.42**
	Location(Habitat)	12	2.32	3.30**	31.38	3.60**
	Residual	60	0.70		0.38	
	Total	74				
	Cochran's test		ns, 0.1918		ns, 0.2141	
	Transformation		Ln(x+1)		Ln(x+1)	
	Pair-wise comparisons			N diff. B* N diff. C*		N diff. B** N diff. C***
<i>M. neritoides</i>	Habitat	2	2.28	3.84*	0.91	0.79
	Location(Habitat)	12	0.60	3.57**	1.15	7.11***
	Residual	60	0.17		0.16	
	Total	74				
	Cochran's test		ns, 0.1905		ns, 0.1377	
	Transformation		X ^{0.1}		X ^{0.1}	
	Pair-wise comparisons			N diff. B* B diff. C*		
<i>C. stellatus</i>	Habitat	2	17.25	4.66*	0.11	0.16
	Location(Habitat)	12	3.70	5.39***	0.70	4.97***
	Residual	60	0.69		0.14	
	Total	74				
	Cochran's test		ns, 0.2250		ns, 0.1122	
	Transformation		Ln(X+1)		X ^{0.1}	
	Pair-wise comparisons			N diff. B*		
		df	Mid-shore		Low-shore	
			MS	<i>F</i>	MS	<i>F</i>
<i>Patella</i> spp.	Habitat	2	3.07	0.94	0.05	0.17
	Location(Habitat)	12	3.28	4.52***	0.31	2.57*
	Residual	60	0.73		0.12	
	Total	74				
	Cochran's test		ns, 0.1873		ns, 0.1866	
	Transformation		Ln(X+1)		X ^{0.1}	
	Pair-wise comparisons					

Table 5 Two-way ANOVA comparing the numbers of faunal species (density of *T. striatus*, *M. neritoides* and *Patella* spp. and percent cover of *C. stellatus*) between roughness (Smooth surface S, Rough surface R) and sites (Site 1, S1; Site 2, S2) at different intertidal levels.*** $P < 0.001$.

	Source	df	Mid-shore		Upper-shore	
			MS	<i>F</i>	MS	<i>F</i>
<i>T. striatus</i>	Roughness	1	17.02	18.35***	35.81	28.84***
	Site	1	0.84	0.91	0.27	0.22
	Pooled Data	17	0.93		1.24	
	Total	19				
	Cochran's test		ns, 0.5710		ns, 0.5099	
	Transformation		Ln(x+1)		sqrt(x+1)	
<i>M. neritoides</i>	Roughness	1	3.98	4.46		
	Site	1	0.25	1.67		
	Roughness x Site	1	0.89	6.05*		
			(S1, R>S***; S2, R=S)			
	Residual	16	0.15			
	Total	19				
	Cochran's test		ns, 0.4034			
	Transformation		X ^{0.1}			
<i>Patella</i> spp.	Roughness	1	22.05	0.84		
	Site	1	4.05	0.15		
	Pooled Data	17	26.40			
	Total	19				
	Cochran's test		ns, 0.4715			
	Transformation		None			
<i>C. stellatus</i>	Roughness	1	5313.80	6.69		
	Site	1	405.00	2.71		
	Roughness x Site	1	793.80	5.32*		
			(S1, R<S*; S2, R<S***)			
	Residual	16	149.20			
	Total	19				
	Cochran's test		ns, 0.4871			
	Transformation		None			